

THE POPULATION BIOLOGY OF NEOTROPICAL CICADAS III BEHAVIORAL NATURAL HISTORY OF *PACARINA* IN COSTA RICAN GRASSLANDS¹

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ABSTRACT: Various aspects of behavioral natural history, including habitat selection, seasonal occurrence of adults, eclosion sites and density of nymphal skins, and a variety of diurnal activities of adults including singing, feeding, and oviposition, are described for a species of small *Pacarina* cicada. Studies on this undescribed species were conducted at two localities in northwestern Costa Rica and both habitats were grasslands. At one locality in the lowlands of Guanacaste Province, adults are most abundant during the wet season and at the other locality, which is in the mountains, adults are probably active throughout most of the year. Collections of nymphal skins in lowland Guanacaste support the contention that adult abundance there is very seasonal. Singing activity is most prevalent on clear mornings when the air temperature is still rising and later in the day when it is very hot, feeding and oviposition occur. Adults feed on a variety of shrubs in grasslands and oviposition occurs in dead tissues of grasses and shrubs. The eggs are laid in bifid arrangement within the tissues. The singing behavior is variable in this cicada in that males either sing alone or in small choral groups. Several choral groups can be found and distinguished in a single small tree by asynchrony in singing among the groups. It is suggested that members of a single choral group stay together primarily through visual interactions at close distances on branches. The function of the song in this cicada remains obscure, but it very likely serves to attract females for mating and oviposition. The diurnal singing pattern is influenced greatly by weather conditions. The cryptic coloration and behavior patterns of adults and nymphs are suggested to be adaptations to escape from visual-hunting predators.

DESCRIPTORS: neotropical cicada, Costa Rica, wet season, dry season, grasslands, habitat preference, reproductive behavior, thermoregulatory behavior, choral groups.

Very little is known about the behavioral natural history of cicadas in the Central American tropics. This paper reports various descriptive and experimental studies on a little *Pacarina* cicada (Tibicenidae) conducted in grassland localities in northwestern Costa Rica. Two similar appearing genera of cicadas, *Pacarina* and *Proarna*, contain small to medium-sized mottled grayish-brown species that are most characteristic of dry and often disturbed habitats. *Pacarina* is a dust bowl and dry grassland genus containing small cicadas that are distributed throughout Central America and into the southwestern United States (Beamer, 1928), while *Proarna* contains medium-sized cicadas with a Central and South American distribution. From my studies in Costa Rica over

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the past several years, I have found that *Pacarina* cicadas are most abundant in the northern region and particularly on the Pacific slopes of the Cordillera Centrale and in the dry lowlands of Guanacaste Province. I have not encountered any species on the Caribbean drainage of the Cordillera Centrale nor in the wet lowlands in the northeast. Thus the genus is represented by complexes of species in the northern-Pacific regions of Costa Rica where grassland habitats and now coffee plantations prevail.

In this paper, I present data on the natural history of one species of *Pacarina*, although the species name is not yet available as it is likely a new species (Dr. Thomas E. Moore, pers. comm.). The natural historical data given include: habitat of adults, location of final instar exuviae, oviposition, diurnal activity patterns, and spacing patterns of adults over small portions of their habitat. It is hoped that these observations will be useful in subsequent studies on the population biology and behavior of the genus over a larger geographical region of Central America.

DESCRIPTION OF FIELD STUDIES

The major study site was near Puntarenas, a 20 x 35 meter area (75 m. elev.) of roadside embankment along the eastern side of the Pan-American Highway about three kilometers northeast after the highway divides to Puntarenas; it is about seven kilometers south of the "Barranca site" discussed in Orians (1969) and Janzen (1971). I studied *Pacarina* at this site during the following periods: June 10-12, 1970; July 6-10, 1971; July 25-27, 1971; July 3-6, 1972; January 4-5, 1973; June 18-20, 1973; July 27-29, 1973; December 10-13, 1973; December 25-27, 1973. Usually the site was visited from 8:00 A.M. to 4:00 P.M. (C.S.T.) on each day, and during the 1971-1973 (excluding December), I was accompanied by one or more trained assistants. Air temperature readings were taken at this site several times each day.

The other study site (600 m. elev.), which was visited only for a few successive days during January, 1973, is about four kilometers east of the village of Esparta, along the Pan-American Highway. It is located in the steep lower hills on the Pacific slopes of the Cordillera Central; it is approximately 40 kilometers from the major study site in lowland Guanacaste, but this species of *Pacarina* is found at many places between these two sites. Both localities experience a severe dry season, generally between

January and April, causing most of the woody vegetation to become deciduous, save for patches and strips of forest along permanent streams in gullies. Much of the grass cover in open areas dries up during the dry season at both localities.

Field studies conducted at the Puntarenas site during the 1971 study periods were qualitative notes on: habitat selection by adults, reproductive behavior, and adult abundance. During 1972, a census was made of nymphal skins (exuviae) in a plot of ground along with a record of an emergence plant used by nymphs. Other visits to this site (1970 and 1973) allowed censuses of adult abundance and nymphal skins. It was hoped that these data would provide a preliminary view of seasonality in this cicada, despite lack of quantitative data on population emergences throughout the year. The Esparta site was used to observe chorusing positions along localized topographic gradients created by steep hills. In addition to these studies, observations were also made on diurnal singing, feeding and oviposition patterns, adult positions on plants, and one instance of predation on an adult.

Habitat selection was studied by walking through large areas and noting where males were chorusing. It was also noted as to whether males were singing in trees or grasses, etc. Unlike many other neotropical cicadas, it is possible to approach adult individuals of *Pacarina* within inches to observe feeding, etc. The initial difficulty is spotting the tiny, cryptically-colored cicada among branches or grass stalks.

Reproductive behavior was studied by marking individual cicadas with small spots of bright paint ("Flo-Paque", Floquil Products, Cobleskill, New York) on the dorsal area of the mesothorax, and then observing within-day and day-to-day movements of these marked individuals. The cicada was netted, color-coded, and released immediately at the place of capture; whenever possible, the marked cicada was returned to the perch where it was captured. Individuals were color-coded with a variety of symbols (dots, bars, etc.) and these were translated into numbers in a data book, so that each marked cicada was assigned a number (1-25); the tiny size of the cicada prevented writing numbers directly on them. During the two 1971 study periods, a total of 25 males were marked in this manner and observed on subsequent days. The interest here was to observe how choral groups are formed, positions of choral groups, and the amount of turnover in composition of choral groups. Although this sample

of marked adults is very small, it nevertheless provided some interesting data on location and habits of individuals within a small area of habitat. A larger sample was not taken since (1) we marked most of the individuals in this area for a given day of



Figure 1. Habitats of *Pacarina* in northern Pacific Costa Rica. Rolling, steep hills at the Esparta site, showing the grassland habitat during the dry season (A). Dead tree branches that formed a chorusing site for several males, January 16, 1973, Esparta site (B).



Figure 2. Habitats of *Pacarina* in northern Pacific Costa Rica. View of the Puntarenas study site, showing the thick, dead grass cover (*Dichromena*) during the dry season (A). Scattered trees and shrubs at the Puntarenas site; one boundary of the study plot ran from the highway (right side in A) to the fence posts (B).

observations, and (2) we wanted to minimize general disturbance of the vegetation in the area that might be used as perches for these cicadas. This information provided data on the spacing patterns of singing males in the habitat. Also, the positions of ovipositing females relative to choral groups was also studied. Copulatory behavior and courtship were not observed.

Nymphal skins were censused during 1972 at the Puntarenas site by setting up a 3 x 20-meter quadrat along one side of a steep gully that bounded one side of the study area; this strip extended lengthwise from the highway (at the beginning of the embankment) back to a wire fence. The census technique was to crawl slowly through the quadrat, three workers abreast and working at about the same rate, and examine very thoroughly the bases of dried grass clumps and the litter between clumps. The tiny nymphal skins match the color of dead grass very closely, and every effort was made to be as thorough as possible. The quadrat was a large patch of grass clumps, but also containing a few assorted shrubs, including *Leuhea* sp. (Tiliaceae) and *Tecoma stans* (Bignoniaceae). The most abundant grass here, *Dichromena ciliata* Vahl., was probably only grass in the quadrat and it formed an almost homogeneous cover. The census period ran for six hours on one day. The plot was also examined two times during the 1973 dry season and two additional censuses were taken during the following wet season (June 19 and July 29, 1973).

RESULTS

Habitat Selection and General Biology

At both Esparta and Puntarenas, *Pacarina* is very common in roadside grass patches, where males chorus on bare branches or tall dead grasses (figs. 1, 2). Adults were absent at the Puntarenas site during January and February, but very abundant during June and July; at the Esparta site, they were found during all of these months. In a given area, more than 50% of the chorusing population is found in dead grasses, and when a tree is close by, it becomes a major chorusing site. Very often, fallen dead branches (fig. 1-B) are used as chorusing sites for several males. In all instances, this *Pacarina* selects very sunny spots for a variety of adult activities, including singing, oviposition, and feeding. At Esparta, *Pacarina*, judging from singing males, is most abundant at

the tops of hills and generally absent from the valleys. As pointed out below, such a distribution of adults is due at least in part to the association of nymphs with grasses which predominate in valleys, and not with forests in gullies (fig. 1-A); but another aspect is undoubtedly the fact that adults are active in open, sunny places. The song is a strong, persistent buzz which seems to carry very well in strong winds that blow across hill tops in this region, as well as in the dry lowlands.

Of a total of 20 males observed on a July morning in 1971 at the Puntarenas site, only two were seen feeding at various times from 8:00 A.M. to 12:00 noon; but all of them were feeding after 2:00 P.M. the same day. Nine days of similar observation for six hours daily support the view that *Pacarina* males (a total of 26 additional observations of individuals feeding) generally restrict feeding to afternoon hours when the amount of overcast has increased substantially and singing, although not eliminated, is greatly diminished. Singing is most characteristic of the morning, especially between 8:00 and 10:00 A.M. when the skies are very sunny and clear. The actual diurnal pattern of singing is extremely variable, depending greatly upon daily weather conditions. In the absence of very strong winds, overcast does not diminish singing, but strong winds, on overcast days, are characterized by considerably fewer singing cicadas. Singing is also greatly diminished during the late morning and early afternoon hours on clear, sunny days, during which air temperature may rise from 25°C (at 9:30 A.M.) to 30°C (at 11:30 A.M.) during June or July. On days of heavy overcast, however, singing continues during these hours.

Oviposition is generally confined to late afternoon (4:00 P.M.) on clear, sunny days but occurs throughout the day when there is overcast or light rains. The oviposition behavior is described below. During the 1971 study periods at Puntarenas, a total of 9 females was seen ovipositing in the study area. Like feeding, oviposition occurs at the hottest hours of the day.

Marked males (fig. 3-A) exhibit very localized day-to-day movements. Out of a total of 20 males marked during the period July 6-8, 1971, 14 were registered at least once over the next 2-3 days in the same area. This high incidence of resightings is discussed below in terms of choral group formation, but here, our concern is the spatial distribution of eclosing adults. In the quadrat used to sample nymphal skins, a total of 36 skins (18



Figure 3. General biology of *Pacarina*. Marked male sitting in full sun on a dead branch (A). An exuvium on dead grass stalk (B). The spider *Acanthepeira stellata* feeding on a female *Pacarina* (C).

females, 15 males, and 3 undetermined because crushed) were censused on one day in the 1972 wet season, giving a density of 0.6 cicadas per square meter. All of these skins (fig. 3-B) were fresh and most (28) were still clinging to dead grass stalks, suggesting that emergence was recent. Within the quadrat, the skins were distributed very clearly among three different patches of grass (*Dichromena ciliata*), suggesting a food plant relationship. Judging from (1) the distance to shrubs, (2) the tiny size of the cicada, and (3) the dense but short root systems of the grass, the inference is one of *Dichromena* being the major food plant for *Pacarina* juveniles at this site. Until actual feeding can be observed, this food plant association must remain tentative. Undoubtedly the estimate of density is lower than the real density, since (1) we very likely missed several skins, and (2) hoof impressions made by cattle may have contained a few badly crushed skins which could have been overlooked easily. Although we have not marked recently eclosed adults, it is my impression, based on mark-resight data on older males, that adults are relatively sedentary during their lifetime. Individual mobility is primarily in the form of movement over a small area, and range of movement is determined at least in part by sites of eclosion. The factor promoting the greatest amount of mobility within a study area such as the Puntarenas site is movement between dead grass clumps and succulent tree branches used for feeding. Singing perches and oviposition substrates are dead grass stalks, but this cicada feeds on living shrubs and small trees (fig. 2). Thus, there is movement of both sexes between dead grasses and feeding sites in trees and shrubs. In order to understand this movement pattern, we can make an illustration with marked male no. 4 on July 8, 1971. This individual was marked along with six other males, during the interval 12:10 - 12:30 P.M. Upon release, it flew away and was resighted at 1:45 singing on a tall dead grass stalk about five meters from the place of capture and marking. Once resighted, we watched its movements, along with other marked males, for the remainder of that afternoon. After the initial resighting, male no. 4 was seen 20 minutes later on another dead grass stalk, where it was silent. Ten minutes later, it was found in a small leguminous tree (*Gliridicia sepium*-“Madero negro”) along the fence, where it had the proboscis clearly inserted into a live branch. It remained here for 18 minutes, after which it was seen in another clump of dead grass, singing with two other males. It was seen feeding in

another nearby tree at 3:50. Very similar movements were seen in other marked males on several days.

Although it is very difficult to detect mortality factors operating on adult cicadas, we did make one observation of predation on adult *Pacarina*. At 2:00 P.M. on July 6, 1971, we saw the spider *Acanthepeira stellata* (Walckenaer) feeding on a female *Pacarina* trapped in loose web just beneath the crown of *Dichromena* grass (fig. 3-C). Such predation is probably incidental locally, since sweep samples of nearby areas reveal very few individuals of the spider (personal observations). It is also unlikely that this spider is specialized for feeding on small cicadas such as *Pacarina* since most spiders are generalized predators on a variety of arthropods.

Reproductive Behavior

Pacarina males form small choral groups of usually 2-4 individuals, with members spaced within 2-3 inches of each other (1) side by side on adjacent dead grass stalks, or (2) above one another on thick branches of shrubs and trees. The result of this behavior is that males occur in small patchily-distributed "pockets" where each group may be a few meters from the next one. Also, males sing individually, but in our experience, solitary males may eventually join a choral group, attracted to it apparently by the songs of prior members. Choral groups are most active in the early morning, although singing may also occur in the late afternoon on cooler, overcast days. To give an example of the typical spatial distribution of *Pacarina* choral groups, on one morning (July 8, 1971) there were six different groups of singing males and each group was positioned in a different grass clump or shrub. All of these groups were within the 20 x 35 meter study plot. On occasion, there occur two or more different clusters of singing males within the same small tree; but these groups do not always sing in unison. Sometimes one or more of the groups within a tree are silent while another is chorusing; other times two or three groups chorus without synchrony among them. Sometimes all groups chorus in unison (synchronously). On a single branch the males comprising a single choral group can be spaced out over about a one-meter length; another group would be on a second branch.

One important component of choral group singing in *Pacarina* is the apparent high turnover in membership of the group. From

observing a total of 14 different choral groups over several days, it was found that the average duration of a group is about 40 minutes, and with no difference dependent upon the size of the group. A marked male is a member of a given choral group for an average of 16 minutes, after which he leaves and either assumes a solitary perch or joins another choral group close by the first one. Complete breakdown of a choral group is dependent upon several different factors, of which accidental "bumping" by one male into another causes either some or all individuals to fly away. In the early stages of choral group formation on a given morning, individuals are attracted by the singing of a single male. A good example is the morning of July 9, 1971 when we witnessed the formation of a choral group in a patch of tall, dead grass stalks, just above the embankment. A single marked male (no. 7) was singing at 7:55 when we arrived at the site. Within 10 minutes an unmarked male flew in and landed on an adjacent grass stalk and walked to within 2 inches of the singing male; the second male began to sing within 45 seconds, after walking had ceased. These two males sang for 18 minutes, with intermittent pauses (the mean length of song for male *Pacarina* here is $7+1.4$ minutes, as measured on 10 individuals during a single morning) before a third, and marked male flew to the pair. This was marked male no. 3 and it eventually positioned itself within 3 inches of the other males and also began to sing. When a strong wind would cause singing to stop, usually one male, but not always the same individual, would initiate singing again and the others would then follow suit; there are times, however, when a male remains completely silent while others sing in the group. Between song sessions, there may be considerable walking movements among members of a choral group. Walking involves a very noticeable clicking noise which is characteristic of *Pacarina* and *Proarna* males in general, and it is produced in both forward and backward stepping. Depending on their positions relative to one another, males in a choral group tend to walk towards one another, and often bump into one another. This behavior, when bumping does not occur, tends to tighten up the choral group and perhaps subsequently strengthen the joint acoustical properties of the participants in singing sessions. Walking is prevalent during the early stages of choral group formation, as new males are recruited to the spot where one or more are already singing. Whether or not

the clicking is a means of communication between individuals is unknown.

Marking does not affect choral activities of males. At 8:15 A.M. one day (July 8, 1971) we found a choral group containing four males, two of which were marked (nos. 2 & 7) on the previous day. Marked individuals survive for at least three days, as indicated by our daily resightings (over a three-day period) of 20 out of 25 marked cicadas for the combined July, 1971 study periods. For the first period, the mark-resight data was as follows: nos. 1-7 marked July 7, 6 resighted July 8; nos. 8-13 marked July 8, total of 9 resighted July 9; nos. 14-20 marked July 9, total of 13 resighted July 10. For the second period: nos. 21-23 marked July 27, one (no. 21) resighted July 28; nos. 24-25 marked July 28, total of three resighted July 29. Cicadas marked during the first period were not resighted in the area during the second period, suggesting (1) a life expectancy in male *Pacarina* of less than 20 days, or (2) emigration from the area. Our high percentage of total resightings (80%) for both periods combined suggests residentiality in male *Pacarina* and that these cicadas may live less than 20 days, assuming they were very young at the time of marking during the first period.

Another aspect of reproductive behavior studied was the association of females with choral groups at the Puntarenas site. Females fly to where males are singing and oviposition may begin shortly thereafter. One example illustrates this behavior, although it has been observed only nine times. Two males were singing in dead grass stalks at 9:51 A.M. (July 10, 1971), and three minutes later, a third cicada joined the group. This individual perched on an adjacent grass stalk and walked up and down it for about one minute. The two males continued to sing, raising their abdomens in an arched manner as shown in figure 4-A,B. In the meantime, the third cicada, a female, had begun to oviposit in the grass stalk.

The oviposition posture is very easy to recognize (fig. 4-C,D,E) and eggs are laid only in dead plant tissues. For a total of 13 different oviposition acts witnessed, all of these were in dead plant tissue with 10 of them in dead grass stalks and three in dead branches of shrubs. On the substrate of her choice, the female will make from three to eight tiny holes or pockets (fig. 4-F) with her ovipositor, and deposit several elongate, flattened eggs in each cavity. Each egg is about 1.8 mm long and they are arranged in bifid rows within the dead plant tissue. The number of eggs per cavity varies greatly in our experience, there being from 20 to 35 eggs in each. The total egg productivity of a single female must be over 200, judging from the number of cavities (fig. 4-E) and eggs

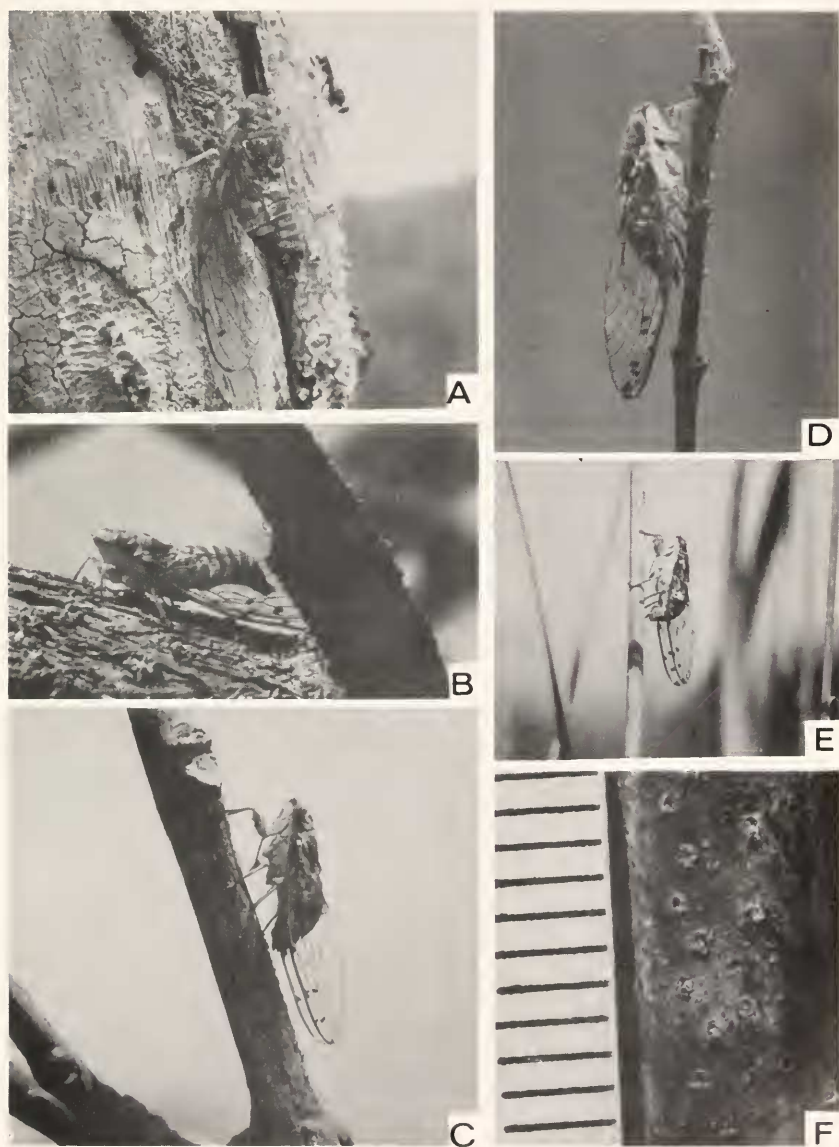


Figure 4. Reproductive behavior of *Pacarina*. The cryptic positioning of a singing male (note arched abdomen) on a tree trunk at the Puntarenas site (A). Lateral view of singing male perched on a dead branch in a fallen tree (see Figure 1-B) at the Esparta site (B); the song of this individual was recorded by T. E. Moore. Females ovipositing in dead branches at the Puntarenas site (C-D). Oviposition in a dead grass stalk at the Puntarenas site (E). Marks of egg pockets (the scale to the left is in mm) in a dead woody stem (F) at the Puntarenas site.

per cavity produced by a single female. Oviposition is usually uninterrupted, and it lasts from 15 to 45 minutes, depending on the number of eggs to be laid and perhaps the toughness of the plant tissue. The female flies away after egg laying is completed.

A most consistent feature of oviposition behavior in *Pacarina* is that it invariably occurs very close to a choral group; females, apparently already mated, fly into the vicinity of the choral group and begin to lay eggs. This pattern has been observed at different times of the day and under a variety of weather conditions; females only fly into the choral group when at least one member is singing. Females do not appear when choral groups are silent. Courtship behavior has not been observed, although it is likely that choral groups function in this aspect of reproductive behavior as well.

Seasonal Adult Abundance

The degree to which *Pacarina* is a seasonal cicada depends greatly upon the region where it is found. For example, at the higher elevations around Esparta, adults may be heard singing in large numbers throughout the year, except during periods of extreme dryness, which occur irregularly in this region of Costa Rica. For lowland Guanacaste, we know that eclosion is high during the wet season and non-existent during the dry season: during the 1973 dry season (which was very severe), the census plot was examined two times for skins and none were found; no adults of this species were heard singing in the area (although another, larger species was seen and heard). Furthermore, during the early part of the following dry season (December, 1973 for the 1974 dry season) no fresh exuviae were found at the Puntarenas study site. The 1972 census data from this plot during the wet season has already been summarized in connection with the food plant. But on a comparable date (June 19) the following year, a total of 36 skins (14 females and 22 males) were again obtained from this plot. Forty days later (July 29), only 18 skins (12 females and 6 males) were found in the plot, suggesting a decline in the emergence at this time. The emergence declines late in the wet season is also indicated by the preponderance of female skins over male skins; other studies of Costa Rican cicadas also showed a similar sex ratio trend in species with strongly seasonal emergence patterns (Young 1972). The very noticeable absence of *Pacarina* adults at the Puntarenas site during the peak of the dry season also suggests that this cicada is essentially a wet season species at this locality. It is not determined whether or not all nymphs of equal

age emerge during one year at either locality, but it is likely that annual emergence patterns are different between Esparta and Puntarenas since adults are probably active throughout most of the year at the former locality.

DISCUSSION

Although we can say very little regarding the initial adaptive radiation of *Pacarina* cicadas at various places along their extensive present-day geographical distribution in Central America, it is nevertheless apparent that most species, including the one studied here, are inhabitants of tropical dry areas such as northwestern Costa Rica. Much of the behavioral aspects of the natural history in selected species are therefore expected to be related to survival and reproduction in seasonally dry tropical habitats such as lowland Guanacaste, Costa Rica.

The species of *Pacarina* studied is probably one of the smallest-sized members of the genus in Central America, and it is therefore interesting that adults are most active during the wet season in lowland Guanacaste rather than during the severe annual dry season of this region. If it is assumed that the preliminary data on emergence from the Puntarenas site is indicative of a wet season adult emergence pattern in this region, there may exist environmental conditions associated with the dry season which preclude this cicada from being very active (i.e., abundant in large numbers) during this season. In the absence of thorough monthly data on annual emergence patterns, the reduction or absence of adult *Pacarina* during the dry months in Guanacaste is indicated by the lack of singing males. It is interesting to also note in this context that another species of *Pacarina*, which is about twice the body length of the species studied (fig. 5), is active in Guanacaste during the dry season (Allen M. Young, unpubl. obs.). If it is assumed that body size is an important factor limiting the activity of insects during tropical dry seasons (Janzen and Schoener, 1968), these preliminary suggest the interesting hypothesis that there is a replacement of *Pacarina* species in at least some areas of lowland Guanacaste: the small species is active primarily during the wet season and the large species is active during the major dry season (December-March). Selection is predicted to favor the small species being active during wetter months as a means of escaping desiccation problems that would prevail for small insects during the dry season. It is more difficult to suggest why the larger species would not also be active during the wet season; further studies with these ideas in mind should perhaps be directed to an

examination of possible competitive interactions between the two cicadas in order to account for the apparent limitation of the large *Pacarina* to the dry season.

Studies on the thermoregulatory behavior of cicadas in the southwestern United States have demonstrated that these insects change their behavior patterns in response to increased air temperatures during the day (Heath and Wilkin, 1970; Heath, Wilkin, and Heath, 1971). In general, these studies revealed that



Figure 5. Large and small species of *Pacarina* from lowland Guanacaste, Costa Rica. The larger species is active during the dry season, while the smaller one is active during the wet season.

adult cicadas will move out of direct sunlight into shade in response to overheating of their bodies. In the present study, it was found that adults of *Pacarina* feed and oviposit at the hottest times of the day, and perhaps this represents a preference for remaining relatively inactive (non-moving) to reduce overheating. Singing is most intense (the greatest numbers are singing in an area) while temperatures are rising during the morning and both sexes are active in courtship before it is too hot. Such diurnal patterns of behavior in *Pacarina* are adaptations for living in hot and dry conditions.

The function of choral groups in *Pacarina* may be related to courtship and oviposition. Acoustically, the grouped singing of several males in unison provides a stronger song that could attract females for courtship. Oviposition occurs near choral groups and eggs are laid in the most abundant vegetation, including dry grasses and dead branches of small shrubs. The song of the individual male is very strong and the necessity of choral groups for acoustical aspects of behavior may be limited in this species of *Pacarina*. This is also suspected from the observation that several males may sing from solitary, scattered positions within a grassland area and choral groups are not the rule. Further evidence in support of this view includes (1) asynchronous singing among different choral groups within the same tree, and (2) the presence of silent individuals in the immediate vicinity of singing by others. All of these observations indicate that *Pacarina* males exploit their acoustical abilities in several different ways, and choral group formation is only one of these. Some singing by individual males may represent an early stage in the actual formation of choral groups: such individuals may be focal points for recruitment of other males. Other instances of males singing alone may be the result of disruption of choral groups resulting from environmental disturbances.

The integrity of a single choral group in a tree may result from visual proximity of individual males. Such a mechanism might be especially important when more than one choral group is present in a tree. Observations indicate that all males within a choral group are in visual contact with one another: when a male begins walking, a nearby individual will often begin to walk away as the first approaches.

The very cryptic nymphs eclose primarily among dead stalks at the bottom of grass clumps and the grass *Dichromena* is the major eclosion plant at the Puntarenas site. Eclosion probably occurs near the bottom of these grass clumps as suggested by the

positions of some exuviae on grass stems; eclosion near the ground may prevent eclosing adults from being knocked off vegetation by gusty winds characteristic of grasslands and also reduce desiccation during the actual molt.

In addition to the final instar nymphs, the adults of this *Pacarina* are cryptically colored and this adaptation could function to reduce predation by visual-hunting predators with color vision. The behavioral pattern of nymphs eclosing on dead grass stalks is one example of crypsis, and the excellent color-matching of the adults by positioning themselves on grayish branches, grass stalks, and fence posts in Guanacaste is another example of behavior undoubtedly associated with escape from predators. But eclosing adults and even nymphs above or just below the soil surface may be prey for a variety of predatory arthropods that do not rely mainly upon visual detection of coloration. Adults, being rather low fliers through grasses and small shrubs in Guanacaste, may become occasionally the prey of a variety of orb spinners such as the case recorded here.

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